Journal of Coastal Research	5	3	477-488	Charlottesville, Virginia	Summer 1989

Trophic Relationship in the Surf Zone During the Summer at Folly Beach, South Carolina[1]

Lawrence B. DeLancey

South Carolina Wildlife and
Marine Resources Department
217 Fort Johnson Road
Charleston, South Carolina 29412, USA

ABSTRACT

DELANCEY, L. B., 1989. Trophic relationships in the surf zone during the summer at Folly Beach, South Carolina. *Journal of Coastal Research*, 5(3), 477-488. Charlottesville (Virginia), ISSN 0749-0208.

Trophic relationships were examined in the surf zone at a beach site in South Carolina during the summer of 1980. Analysis of stomach contents was conducted on the seven most abundant fish species and two most abundant crab species. The fishes, *Anchoa mitchilli, Anchoa hepsetus,* and *Menidia menidia,* were primarily planktivorous, whereas *Menticirrhus littoralis, Trachinotus carolinus,* and *Arius felis* preyed on benthic fauna. *Mugil curema* consumed primarily sand, containing diatoms and detritus. The crabs, *Arenaeus cribrarius* and *Callinectes sapidus*, preyed on benthic organisms. Benthic prey, particularly the mole crab, *Emerita talpoida*, contributed most of the biomass to the higher trophic levels, although other invertebrates and plankton were also important prey items. Comparisons with other studies revealed that this food web was a fairly typical of high energy beaches in the southeastern United States.

ADDITIONAL INDEX WORDS: *Beach survey, feeding patterns, food web, juvenile fishes, relative abundance, resource partitioning, taxonomic composition, tidal and diel effects, trophic relationships, surf zone.*

INTRODUCTION

The surf zone and sandy beach ecosystem of the southeastern United States is an important, yet inadequately studied habitat. A better understanding of the ecology of this system is essential if it to be utilized and wisely protested in the future. Higher trophic relationships of organisms inhabiting the surf zone in this area are partially understood. PEARSE *et al.* (1942) stated that sandy beaches contain a source of prey for fishes moving in with the rising tide. MCFARLAND (1963a) concluded that plankton was a major source of food for fishes at Mustang Island, Texas. FINUCANE (1969) found pelecypods of the genus *Donax* to be the major food items of two species of carangid fishes of the genus *Trachinotus* collected in the surf zone in Florida. LEBER (1982) found *Donax variabilis* and the mole crab, *Emerita talpoida* to be the most important prey items of several species of fishes and crabs in North Carolina. MODDE and ROSS (1983) observed that the numerically dominant juvenile fishes occurring in the surf in Mississippi were primarily planktivorous. NELSON (1986) estimated that predation by fishes in the surf zone in Florida may remove a large portion of the populations of *Emerita talpoida* and mysids. The purpose of the present study was to elucidate trophic relationships, including identification of major prey organisms and to determine how prey are partitioned among predators at Folly Beach, South Carolina, during the summer months when this area serves as a nursery area for several species of fishes (ANDERSON *et al.*, 1977).

MATERIALS AND METHODS

This study was conducted on the northeastern end of Folly Beach (latitude 32°41.0'N, longitude 79°53.8'W), on Folly Island, a barrier island lying approximately 14 km south of Charleston, South Carolina. The study site, a section of beach approximately 100 m in length, is bounded on the northeastern end by a large rocky groin and on the southwestern end by a small wooden groin. The gently sloping beach

88018 received 11 April; accepted in revision 31 August 1988.

[1]Contribution number 81 of the Grice Marine Biological Laboratory and number 263 of the South Carolina Wildlife and Marine Resources Department.

(1 – 2% slope) is composed chiefly of sand and broken shell. The presence of a series of offshore sandbars partially protects the beach from full wave action. A large trough (approximately 1 m depth) was often present at low tide during the study. Tides ranged from – 0.2 to 2.0 m from mean low water during the study period of 28 June to 26 November 1980. The height of the seas ranged from about 0.1 to 1.0 m during sampling.

Samples were collected at roughly biweekly intervals during the five month study period. During each sampling period a 19.8 by 1.8-m, 9-mm stretch mesh nylon bag seine was used to collect four samples at roughly six-hour intervals. This scheme ensured that both high and low tidal stages and day and night periods were sampled. Samples were usually collected near slack tide (within one hour of either high or low tide), when current velocity was low. The seine was hauled parallel to the beach for a distance of about 100 m in depths of about 1 m. After the seine was beached, organisms were removed and placed directly into full strength formalin, to which seawater was then added to obtain a final concentration of approximately 10% formalin. Larger fishes were incised to ensure preservation of stomach contents. One large collection of white mullet, *Mugil curema*, was subsampled for analysis in the laboratory after a total count was made on the beach. Following each collection water temperature (± 1.0 °C) and salinity (± 1.0 ‰) were measured. Samples of plankton were collected with two 30-cm mouth plankton nets of 500-μm and 100-μm mesh size respectively, towed parallel to the beach, and samples of benthic infauna were collected with a 10-cm diameter metal corer on transects from high tide levels down to subtidal areas on the beach in an effort to examine prey selectivity (DELANCEY, 1984, 1987).

Fishes and macroinvertebrates collected by seine were generally identified to species and enumerated in the laboratory. A total weight (± 0.1 g) for each species in every collection was obtained after blotting the specimens dry. A maximum and minimum measurement (± 1 mm) was obtained for the following: standard length (SL) for each species of fish, total length (TL) for each species of shrimp, and carapace width (CW) for each species of crab.

The seven most abundant species of fish and the two most abundant species of crab were analyzed for gut contents. Stomachs of predatory fishes were removed and their contents washed into a vessel for microscopic examination. Stomach contents of each species were pooled by collection, and only collections containing sufficient numbers of specimens to warrant further analysis were utilized. Stomach contents of the gulf kingfish, *Menticirrhus littoralis,* were also pooled by size class. Food items were sorted to the lowest feasible taxonomic category, with sediment and unidentifiable, partially digested material being placed in separate categories. For planktivorous species, stomach contents were divided into different size fractions by washing them through a series of standard sieves. Smaller prey items were subsampled with a plastic 1.5-ml pipette (a 10% subsample was counted) to estimate taxonomic composition (CARR and ADAMS, 1972). Food material was dried at 60°C for 18-36 hr to constant weight, then weighed (± 0.1 mg). These values were used to calculate a percentage composition of diet by dry weight, excluding unidentifiable, partially digested material and sediment. For *Mugil curema* and the portunid crabs *Arenaeus cribrarius* and *Callinectes sapidus*, the gut contents were examined and the type of food was noted in order to obtain a percentage frequency of occurrence of food items by collection.

The Mann-Whitney U test was used to analyze the possible effects of time of day or tidal stage on abundance of important species, and the Kruskal-Wallis test was used to test the effects of time of day and tidal stage in combination on abundance of the major species (SIEGEL, 1956). Normal cluster analysis using the Bray Curtis coefficient and flexible sorting ($\beta = -0.25$) was conducted on the diets (determined by the number of occurrences of food items after pooling and standardization of data) of the seven most abundant species of fishes, in order to examine similarities in feeding patterns (CLIFFORD and STEPHENSON, 1975; SEDBERRY, 1983).

RESULTS

Water temperature ranged from 13.0 to 31.5°C, whereas salinity ranged from 26.5 to

34‰. A total of 2,391 fishes (representing 24 families and 45 species) and 640 macroinvertebrates (representing nine families and 18 species) were taken in 52 collections. The 10 most important species by number, weight, and frequency of occurrence represented 85.8% of the total catch by number (Table 1).

The most abundant organism collected was the bay anchovy, *Anchoa mitchilli* (27-61 mm SL) which was more than twice as numerous as the next most abundant species. Other abundant fishes included *Menticirrhus littoralis* (21-226 mm SL), *Mugil curema* (46-172 mm SL), the striped anchovy, *Anchoa hepsetus* (31-80 mm SL), the Florida pompano, *Trachinotus carolinus* (19-135 mm SL), the Atlantic silverside, *Menidia menidia* (39-89 mm SL), and the hardhead catfish, *Arius felis* (36-260 mm SL). *Mugil curema* ranked first in biomass. The speckled crab, *Arenaeus cribrarius* (12-55 mm CW), was the most abundant and frequently collected species of macroinvertebrate. The penaeid shrimp, *Trachypenaeus constrictus* (26-56 mm TL) was abundant in seining collections, whereas the blue crab, *Callinectes sapidus* (19-166 mm CW), was not numerous, but ranked second in overall biomass.

The relative abundance of each of these species, with the exception of *Arenaeus cribrarius* and *Mugil curema*, appeared to be influenced by time of day or tidal stage, or the combination of these two factors (Table 2). *Menticirrhus littoralis*, for example, was collected in significantly greater abundance on high tide than on low tide. Generally more organisms, more species, and a greater total weight were collected on low tide than on high tide (Table 3). Greater numbers of organisms were collected during daylight, but larger organisms were collected at night.

A total of 996 stomachs of fishes and crabs were analyzed in this study (Tables 4 and 5). Unidentifiable, partially digested material and sand and broken shell comprised at least 13.6% and 15.7%, respectively, of the total weight of stomach contents of the six species analyzed for dry weight. The following sections address identifiable food items, exclusive of the two categories mentioned above.

The six species of predatory fishes can be categorized as feeders chiefly on either zooplankton or benthic macroinvertebrates. Under the first category, *Anchoa mitchilli* consumed primarily (in decreasing order of importance) brachyuran megalopae, copepods, and mysids (Table 4). *Anchoa hepsetus* had a similar diet, ingesting chiefly brachyuran megalopae, mysids, and copepods, in addition to brachyuran zoeae and amphipods. *Menidia menidia* fed on mysids, insects, an isopod *Sphaeroma quadridentatum*, brachyuran megalopae, and amphipods.

Among benthic feeders, *Menticirrhus littoralis* fed chiefly on *Emerita talpoida*, haustoriid amphipods, reptantians (undifferentiated remains of brachyuran crabs and *Emerita*), pelecypod siphons, and polychaetes. *Trachinotus carolinus* ingested primarily *Sphaeroma*, haustoriid amphipods, the scorched mussel, *Brachidontes exustus*, and *Emerita*. *Arius felis* consumed reptantians, *Emerita*, penaeid shrimp, molluscs, polychaetes, and *Sphaeroma*.

Normal cluster analysis revealed that the two species of anchovies had the greatest overlap in diet, that the two groups of predators were fairly distinct in their diets, and that *Mugil curema*, primarily a feeder on diatoms and det-

Table 1. *Number of individuals (N), weight (g), and percent frequency of occurrence (F) of the most important species collected by seine at Folly Beach. Fi = Fish, B = Brachyuran crab, P = Penaeid shrimp.*

Species	N	Weight	F
Anchoa mitchilli (Fi)	827	756.6	56
Menticirrhus littoralis (Fi)	380	1,331.6	77
Arenaeus cribrarius (B)	365	355.4	77
Mugil curema (Fi)	334	5,010.6	44
Anchoa hepsetus (Fi)	244	445.9	39
Trachinotus carolinus (Fi)	130	813.6	48
Menidia menidia (Fi)	115	286.1	58
Trachypenaeus constrictus (P)	107	46.4	19
Arius felis (F)	67	1,511.2	15
Callinectes sapidus (B)	33	3,162.0	25

Table 2. *Number of individuals (N), percent frequency of occurrence (F), and results of statistical analysis of the most important species collected by seine, according to time of day and tidal stage. Kruskal-Wallis test detected differences among numbers in collection groups. Mann-Whitney U test detected differences between numbers collected during day (D) versus night (Nt), and high tide (H) versus low tide (L).*

	Collection groups								Statistical results		
	High tide Day		High tide Night		Low tide Day		Low tide Night		Kruskal-Wallis	Mann-Whitley	
Number of collections	15		11		14		12				
Species	N	F	N	F	N	F	N	F		D vs NT	H vs L
Anchoa mitchilli (Fi)	300	27	4	36	452	79	71	83	*	NS	NS
Menticirrhus littoralis (Fi)	210	80	116	100	26	57	28	75	*	NS	*
Arenaeus cribrarius (B)	142	60	36	73	74	86	113	92	NS	NS	NS
Mugil curema (Fi)	111	53	42	55	176	43	5	25	NS	NS	NS
Anchoa hepsetus (Fi)	13	13	7	9	202	86	22	42	*	*	*
Trachinotus carolinus (Fi)	19	53	91	73	9	43	11	25	*	NS	*
Menidia menidia (Fi)	25	67	29	73	59	71	2	17	*	NS	NS
Trachypenaeus constrictus (P)	4	7	6	9	—	—	97	67	*	*	*
Arius felis (Fi)	1	7	3	9	1	7	62	42	*	*	NS
Callinectes sapidus (B)	1	7	2	18	9	29	21	50	*	NS	*

Fi = Fish, B = Brachyuran crab, P = Penaeid shrimp,
NS = not significant, * = significant (P ≤ 0.05).

Table 3. *Total number, total weight, and number of species of fishes and macroinvertebrates collected by seine, according to time of day and tidal stages. Kruskal-Wallis test detected differences among numbers, weights, and number of species observed in collection groups. Mann-Whitney U test detected differences between numbers, weights, and number of species collected during day (D), versus night (Nt), and high tide (H) versus low tide (L).*

	Collection Groups				Statistical Results		
	High Tide Day	High Tide Night	Low Tide Day	Low Tide Night	Kruskal-Wallis	Mann-Whitney	
Number of Collections	15	11	14	12		*D vs Nt*	*H vs L*
Fishes							
Number	698	353	1,035	305	NS	NS	NS
Weight (g)	1,913.7	3,285.0	6,685.9	3,257.9	NS	NS	NS
Number of Species	14	15	30	33	*	NS	*
Macro-invertebrates							
Number	153	52	108	327	*	NS	*
Weight (g)	225.0	282.3	1,245.0	1,977.5	NS	NS	NS
Number of Species	7	6	12	15	*	*	*

NS = not significant, * = significant (P ≤ 0.05)

ritus, had no recognizable similarity to the other species in diet (Figure 1).

Some diurnal differences were detected in the feeding of the two species of anchovies (Figures 2 and 3). Both species consumed proportionately fewer copepods and brachyuran zoeae at night than during the day, whereas consumption of brachyuran megalopae was greater during the night. *Anchoa hepsetus* appeared to consume a smaller variety of organisms at night, although only 13 specimens were analyzed from night collections.

Trachinotus carolinus also demonstrated possible diurnal feeding differences. It consumed greater amounts of prey and more diverse prey items during daylight than at night. During the day 29 specimens consumed 119.0 mg of food, in nine prey categories, whereas 80 specimens

Table 4. *Composition of diet of six species of predatory fishes collected at Folly Beach, as analyzed by dry weight and frequency of occurrence (F).*

Prey	*Anchoa mitchilli*		*Anchoa hepsetus*		*Menidia menidia*		*Menticirrhus littoralis*		*Trachinotus carolinus*		*Arius felis*	
	% Wt.	% F	% Wt.	% F	% Wt.	% F	% Wt.	% F	% Wt.	% F	% Wt.	% F
Nemertinea	—	—	—	—	—	—	+	6	+	—	—	—
Nematoda	—	—	—	—	—	—	+	18	+	5	—	—
Annelida												
Polychaeta	—	—	—	—	—	—	2.7	47	+	5	5.0	43
Mollusca	—	—	—	—	—	—	—	—	—	—	9.0	29
Pelecypoda	—	—	—	—	—	—	+	18	5.3	26	—	—
Pelecypod siphons	—	—	—	—	—	—	3.0	77	—	—	—	—
Donax variabilis	—	—	0.4	20	—	—	—	—	—	—	—	—
Brachidontes exustus	—	—	2.1	20	—	—	—	—	20.7	11	—	—
Arthropoda												
Crustacea	0.9	9	7.0	10	—	—	+	24	+	11	0.6	29
Copepoda	27.2	100	11.7	60	2.9	30	+	12	—	—	—	—
Cirripedia	—	—	—	—	—	—	—	—	+	5	—	—
Cirriped cypris	0.3	18	0.1	10	—	—	—	—	—	—	—	—
Cumacea	+	9	—	—	—	—	+	18	—	—	—	—
Amphipoda	0.7	27	7.2	60	8.7	30	0.2	24	+	5	0.2	29
Haustoriidae	—	—	—	—	+	10	13.3	65	24.0	53	0.8	29
Mysidacea	18.1	36	19.5	50	42.0	30	1.8	53	—	—	—	—
Isopoda	+	9	1.4	40	—	—	0.4	24	3.3	11	+	14
Sphaeroma quadridentatum	—	—	—	—	14.5	20	1.6	35	27.3	16	4.8	43
Stomatopoda	—	—	—	—	—	—	—	—	—	—	1.2	14
Stomatopod alima	—	—	—	4.5	40	—	—	—	—	—	—	—
Decapoda	—	—	—	—	—	—	—	—	—	—	0.6	14
Penaeidae	—	—	—	—	—	—	—	—	—	—	9.4	14
Penaeid larvae	—	—	+	20	—	—	—	—	—	—	—	—
Caridean larvae	1.4	46	2.9	50	—	—	—	—	—	—	—	—
Ogyrides alphaeorostris	—	—	—	—	—	—	0.2	6	—	—	—	—
Reptantia	—	—	+	10	—	—	3.3	35	4.7	5	34.5	71
Emerita talpoida	—	—	4.2	10	2.9	10	73.2	59	9.3	16	31.1	43
Brachyuran zoeae	2.2	18	8.3	50	—	—	—	—	—	—	—	—
Brachyuran megalopae	48.3	64	30.7	90	11.6	50	0.1	41	—	—	—	—
Insecta	—	—	—	—	17.4	40	—	—	5.3	11	—	—
Chordata												
Urochordata	—	—	—	—	—	—	—	—	—	—	2.0	14
Vertebrata												
Osteichthyes	—	—	—	—	—	—	+	12	—	—	0.8	14
Larvae of Osteichthyes	0.9	18	—	—	—	—	—	—	—	—	—	—
Total weight of prey (mg)	114.9		71.9		69.0		2,261.0		150.0		4,561.0	
Number of specimens	234		134		89		217		109		13	
Size range (mm SL) of fishes examined for feeding	26–54		31–80		39–80		21–226		20–135		145–238	
Number of collections	11		10		10		17		19		7	

+ indicates presence.

examined for feeding at night consumed only 31.0 mg of food in seven categories.

An apparent effect of tidal stage was noted with regard to the feeding of *Menticirrhus littoralis* (Figure 4). Greater amounts of haustoriid amphipods were consumed by specimens collected at high tide, whereas those collected at low tide had ingested more pelecypod siphons, reptantians, and mysids. Biomass of *Emerita* in stomachs was considerable during both high and low tide, although overall, less biomass was consumed by *Menticirrhus littoralis* during low tide.

An analysis of feeding of *Menticirrhus littor-*

Table 5. *Composition of diet of the white mullet, Mugil curema, the blue crab, Callinectes sapidus, and the speckled crab, Arenaeus cribrarius, as analyzed by frequency of occurrence (F).*

Food	*Mugil curema* % *F*	*Callinectes sapidus* % *F*	*Arenaeus cribrarius* % *F*
Diatoms	64	—	—
Detritus	64	—	—
Annelida			
Polychaeta	—	—	14
Mollusca			
Pelecypoda	—	33	57
Brachidontes exustus	—	83	—
Arthropoda			
Crustacea			
Sphaeroma quadridentatum	—	—	43
Haustoriidae	—	—	29
Natantia	—	—	29
Reptantia	—	33	57
Emerita talpoida	—	—	-
Invertebrata	45	33	14
Chordata			
Osteichthyes	—	67	—
Number of specimens	179	16	75
Size range (mm)	46–137 (SL)	103–150 (CW)	12–52 (CW)
Number of collections	11	6	7

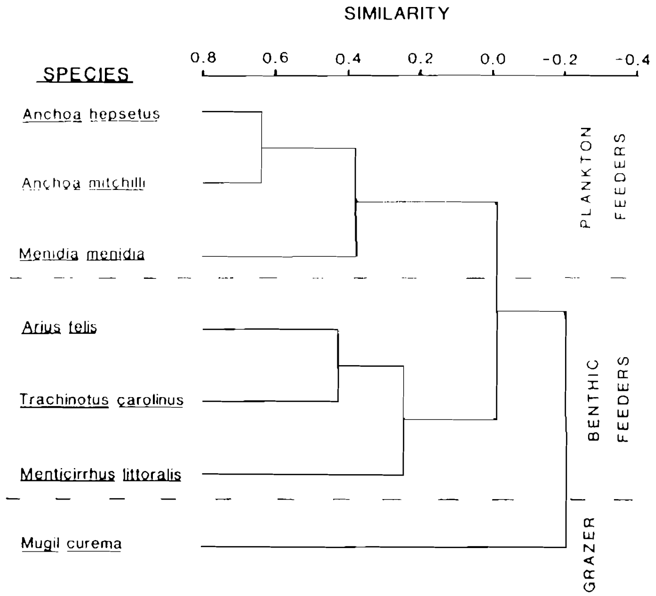

Figure 1. Dendrogram of feeding of the most abundant species of fishes resulting from normal cluster analysis conducted on log transformed, standardized data (frequency of occurrence of food items) using flexible sorting with $\beta = -0.25$ and the Bray-Curtis similarity coefficient.

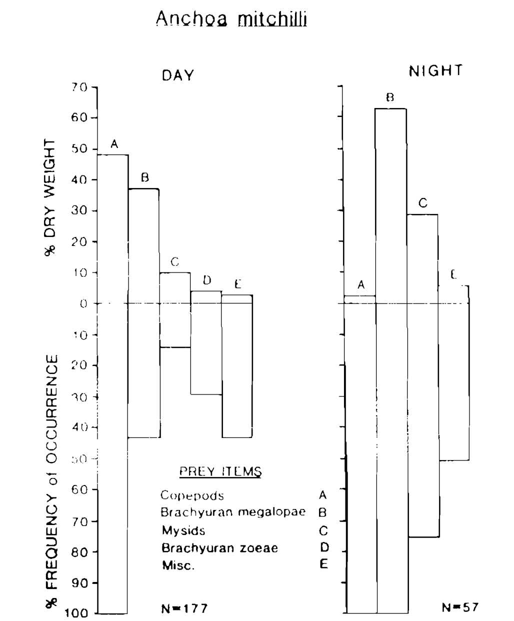

Figure 2. Temporal comparisons of the diet of the bay anchovy, *Anchoa mitchilli*, analyzed by percentage composition of dry weight and frequency of occurrence of food items.

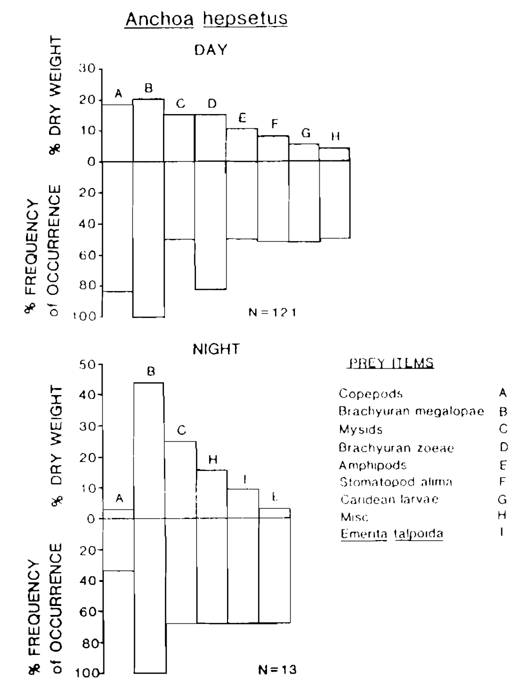

Figure 3. Temporal comparisons of the diet of the striped anchovy, *Anchoa hepsetus*, analyzed by percentage composition of dry weight and frequency of occurrence of food items.

alis by size class revealed that *Emerita* increased in importance with an increase in size of fish, whereas haustoriid amphipods and mysids declined in importance (Figure 5).

The diet of *Mugil curema, Callinectes sapidus*, and *Arenaeus cribrarius* is summarized in Table 5. *Mugil curema* primarily ingested sand that contained diatoms and detritus, although unidentified invertebrate parts were also frequently ingested. *Callinectes sapidus* fed primarily on mussels (*Brachidontes*), fishes, and unidentified invertebrates. *Arenaeus cribrarius* consumed primarily benthic crustacea and other invertebrates.

DISCUSSION

The fauna collected by seine in this study can be considered typical of sandy beaches and high salinity estuaries in the southeast, especially during the warmer months (MODDE and ROSS, 1981; WILLIAMS, 1984; ROSS *et al.*, 1987). Physical factors such as time of day and tidal stage apparently influenced species composition and relative abundance of organisms collected by seine; this too has been demonstrated in other areas (HORN, 1980; MODDE and ROSS, 1981). Biological factors such as prey availability also probably influenced the movements of animals into the surf zone.

Three basic feeding types were detected among abundant organisms collected by seine. The three types were feeders on zooplankton, feeders on benthic macroinvertebrates, and feeders on diatoms and detritus. These results are similar to the findings of other studies conducted on these species. *Anchoa mitchilli*, which has been studied primarily in estauries, has been shown to consume copepods, mysids, and other invertebrates, as well as fishes (DARNELL, 1958; ODUM and HEALD, 1972; SHERIDAN, 1978). Local conditions seem to dictate the source of prey items for this species; benthic organisms were consumed in Lake Ponchartrain, Louisiana (DARNELL, 1958) and North River, Florida (ODUM and HEALD, 1972), but zooplankton and decapod larvae constituted a larger portion of the diet of bay anchovies collected in Apalachicola Bay, Florida (SHERIDAN, 1978) and in this study.

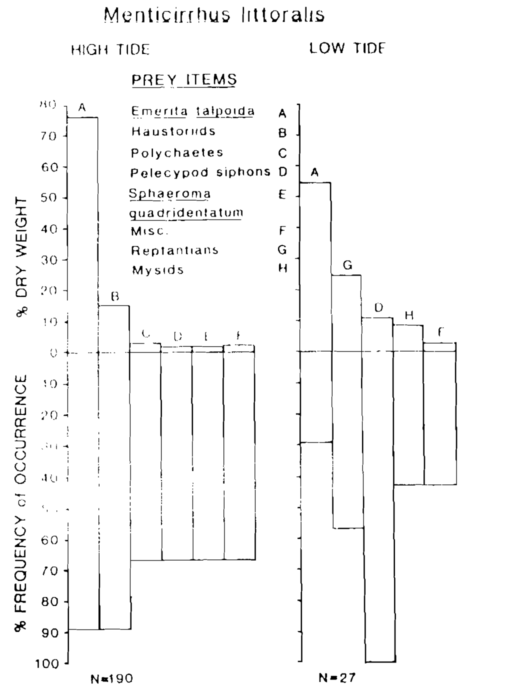

Figure 4. Comparisons of the diet (high tide vs. low tide) of the gulf kingfish, *Menticirrhus littoralis*, analyzed by percentage composition of dry weight and frequency of occurrence of food items.

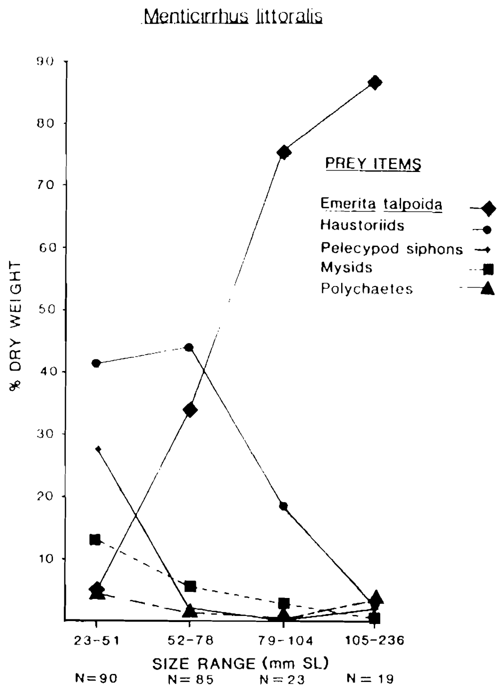

Figure 5. Analysis of percentage composition of dry weight of food items in stomachs of the gulf kingfish, *Menticirrhus littoralis*, according to size.

The times of greatest occurrence of *Anchoa mitchilli* in the surf zone (low tide) coincided with greatest abundance of adult copepods and larvae of *Palaemonetes* (DELANCEY, 1984; 1987). Like *Anchoa mitchilli*, the specimens of the striped anchovy, *Anchoa hepsetus*, examined in this study consumed more brachyuran megalopae than previously reported, although the consumption of other prey such as copepods, peracarid crustaceans, and small molluscs has been observed (CARR and ADAMS, 1973; MODDE and ROSS, 1983). The distribution of *A. hepsetus* within collections was simlar to that of *A. michilli*; it was most abundant during low tide, when prey items such as copepods and caridean larvae were also abundant. Likewise, *A. hepsetus* underwent an apparent shift to larger prey at night, e.g. brachyuran megalopae. These two species of anchovies may undergo a similar response toward selection of prey items that are most abundant during particular stages of the tidal and diel cycles, as suggested in part by HOBSON and CHESS (1976) and MODDE and ROSS (1983). MODDE and ROSS (1983) found that *A. hepsetus* fed primarily during the day in the surf zone in Mississippi; in contrast it exhibited some nocturnal feeding at Folly Beach.

The silverside, *Menidia menidia*, consumed proportionately more peracarid crustaceans and insects but fewer copepods and megalopae than did the anchovies. MOORE (1968) also found the silverside to feed on mysids, amphipopds, and isopods in addition to invertebrate eggs and copepods in Delaware, whereas MCDERMOTT (1983) found that polychaetes were primary food items in the surf zone in New Jersey. *Menidia menidia* demonstrated some feeding activity at night at Folly Beach, in contrast to the findings of KALTES (1984) who found this species to be inactive at night in Rhode Island. At Folly Beach, the silverside was common at all times except on nocturnal low tides. Prey items were abundant during these periods. The absence of silversides from the surf zone during these periods may have been in response to increased abundance of piscivorous fishes in the surf zone during these times. The Atlantic needlefish, *Strongylura marina*, and the bluefish, *Pomatomus saltatrix* were collected almost exclusively during nocturnal low tides. MCDERMOTT (1983) found that *P. saltatrix* fed heavily on *Menidia* in the surf zone in New Jersey. Although it has not been reported in the surf zone, such avoidance behavior has been seen in fish assemblages inhabiting coral reefs (HOBSON, 1975). The fact that the isopod, *Sphaeroma*, and larval insects were important prey items for this species indicates that the silverside fed on the rocky groin community in the study area.

The second basic feeding type encountered in this study was composed of benthic predators. The mole crab, *Emerita talpoida*, the most important prey item consumed by *Menticirrhus littoralis* at Folly Beach, was also found to be a major prey item in the surf zone in North carolina (LEBER, 1982). BEARDEN (1964) found that adult *M. littoralis* in South Carolina also consumed mole crabs, in addition to fishes and stomatopods, whereas juveniles primarily consumed amphipods. In this study *M. littoralis* demonstrated an apparent shift to larger prey items with increasing size, switching from primarily haustoriid amphipods to mole crabs. MODDE and ROSS (1983) also observed a change in diet with size of *M. littoralis* in Mississippi, from mysids to larger invertebrates and fishes. MODDE and ROSS (1983) noted that *M. littoralis* fed more at night, whereas at Folly Beach this species fed during both day and night.

The diet of the Florida pompano, *Trachinotus carolinus*, analyzed in this study closely agrees with the findings of FINUCANE (1969), who examined pompano in the area of Tampa Bay, Florida. In both instances, within similar size ranges of specimens, amphipods (haustoriids at Folly Beach), insects, pelecypods, and crustaceans (*Sphaeroma* and *Emerita* in this study) were the primary prey items. The presence of insects, *Sphaeroma*, and mussels indicate that this species, like *Menidia menidia*, fed on the rocky groin community. That pompano were collected in greater abundance during high tide may be an indication that they rely on the inundated beach and groin areas as a major source of food. MODDE and ROSS (1983) found that pompano of comparable size to those analyzed from Folly Beach also consumed *Emerita*, in addition to shrimp and fish, in the surf zone in Mississippi, whereas smaller specimens (11-40 mm SL) ingested pelecypod siphons, polychaetes, and copepods. As at Folly Beach, MODDE and ROSS 1983) observed that pompano fed chiefly during daylight.

Another species of fish that fed on the benthos at Folly Beach was the hardhead catfish, *Arius felis*. In studies in which stomach contents of individuals exceeding 100 mm SL were analyzed (as in this study), hardhead catfish have been shown to feed primarily on crabs and shrimp, and occasionally mysids, insects, and some fishes (KNAPP, 1949; DARNELL, 1958; HARRIS and ROSE, 1968; ODUM and HEALD, 1972). These results are similar to observations made at Folly Beach, in that *Emerita* and other reptantians (including soft-shelled brachyuran crabs) in addition other invertebrates were consumed. The almost exclusive occurrence of hardhead catfish in collections made at night, although partially due to gear avoidance during daylight, may also be indicative of a pattern in which relatively large species enter the surf zone at night to feed on subtidal and intertidal invertebrates and smaller fishes (ROSS *et al.*, 1987).

The white mullet, *Mugil curema*, represents the third feeding type encountered among organisms collected by seine; it fed chiefly on sand containing datoms and detritus, although some invertebrate parts were also consumed. These results are similar to the findings of ODUM (1970) for the striped mullet, *Mugil cephalus* which consumed primarily diatoms and detritus on the beach at Sapelo Island, Georgia.

Arenaeus cribrarius was found to primarily consume *Emerita* and *Sphaeroma* in this study. LEBER (1982) also observed that *Arenaeus cribrarius* consumed *Emerita* in the surf zone in North Carolina. Like *Menticirrhus littoralis*, the surf zone represents a nursery area for *Arenaeus*, providing both a feeding area and some refuge (ANDERSON *et al.*, 1977; WILLIAMS, 1984).

The blue crab, *Callinectes sapidus*, consumed mussels, other invertebrates (chiefly crustaceneans), and fishes, which is in close agreement with previous studies (DARNELL, 1958; TAGATZ, 1968; ODUM and HEALD, 1972). In this tudy the blue crab was assumed to be a predator, but it may well have been partly necrophagous.

CONCLUSIONS

A proposed food web for the organisms at Folly Beach during the summer months is presented in Figure 6. Prey organisms connected by lines to predatory species represent the primary prey items for each predator. In this study no attempt was made to measure the rate of energy flow through the ecosystem, but rather the attempt was made to define the direction of energy flow to higher trophic levels.

In terms of relative importance, the benthic community probably contributes most of the carbon to the higher trophic levels. Benthic prey items, such as *Emerita*, constituted the bulk of the total dry weight of prey organisms (Table 3). Abundant benthic feeders constituted approximately two-thirds of the biomass of the seining collections (Table 1). The white mullet, primarily a grazer, constituted roughly 27% of the seining catch examined for feeding, whereas about 8% of the catch was comprised of planktivores.

This general scheme of relative importance agrees well with WOLCOTT (1978); LEBER (1982); and MCDERMOTT (1983) who concluded that the benthic macrofauna contributes most of the energy required by the higher consumers in the surf zone and on the beach. My study also implies that the plankton, recognized by PEARSE *et al.* (1942); MCFARLAND (1963a and b); MODDE and ROSS (1983); and NELSON (1986) as major food source, is an important link between the lower trophic levels and the higher consumers in this system.

ACKNOWLEDGEMENTS

This research was completed in partial fulfillment of the requirements for the M.S. degree from the College of Charleston and the Charles-

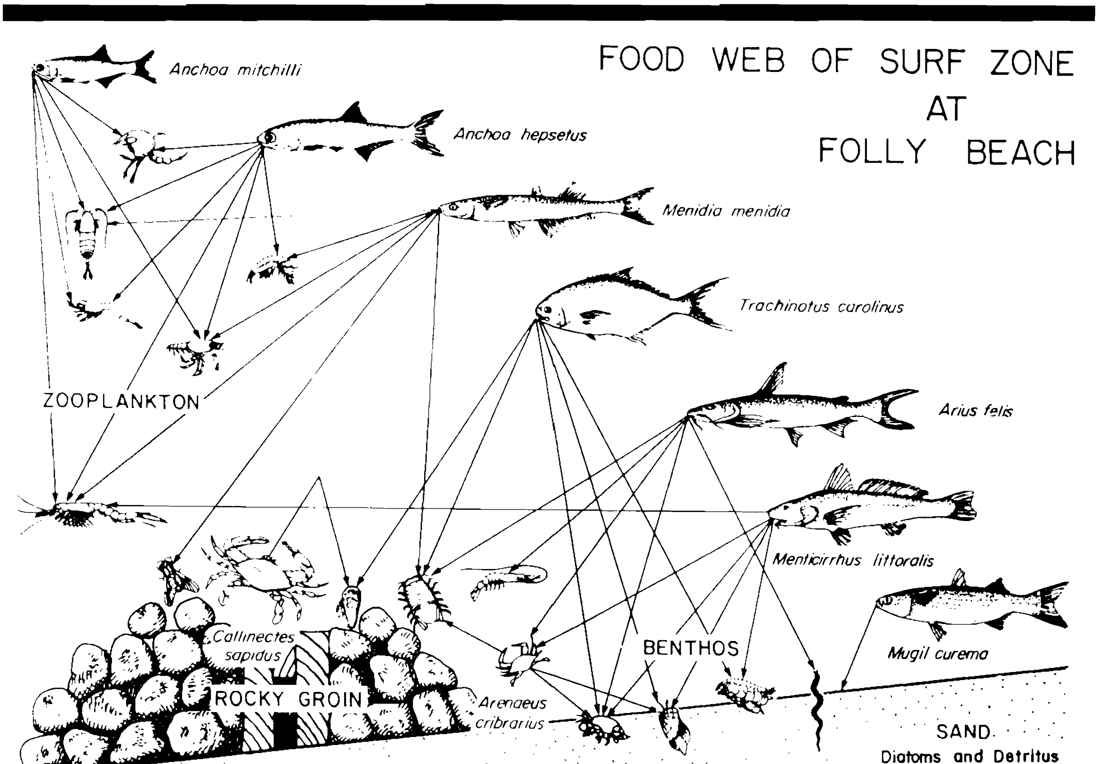

Figure 6. Food web of organisms occurring in the surf zone at Folly Beach, South Carolina.

ton Higher Education Consortium. Support for this research was provided by College of Charleston teaching and research assistanships. I thank my committee members: N. A. Chamberlain, C. K. Biernbaum, E. L. Wenner, and W. D. Anderson, Jr. I thank the numerous individuals who assisted in field sampling, notably F. Blum and M. Chasar, and those who aided in identification of organisms, particularly D. Knott. K. Swanson and B. Stone assisted in preparation of figures, and L. Hammes typed portions of the manuscript. G. Sedberry and W. D. Anderson, Jr. commented on the manuscript.

LITERATURE CITED

ANDERSON, W. D., JR.; DIAS, J. K.; DIAS, R. K.; CUPKA, D. M. and CHAMBERLAIN, N. A., 1977. *The macrofauna of the surf zone off Folly Beach, South Carolina*. NOAA Technical Report NMFS SSRF-704, 23p.

BEARDEN, C. M., 1964. *A contribution to the biology of the king whitings, genus Menticirrhus, of South carolina*. Bears Bluff Contribution 38, 22p.

CARR, W. E. S. and ADAMS, C. A., 1972. Food habits of the juvenile marine fishes: evidence of the cleaning habit of the leatherjacket, *Oligoplites saurus* and the spottail pinfish, *Diplodus holbrooki*. *Fishery Bulletin*, 70, 1111–1120.

CARR, W. E. S. and ADAMS, C. A., 1973. Food habits of juvenile marine fishes occupying seagrass beds near Crystal River, Florida. *Transactions of the American Fisheries Society*, 102, 511–540.

CLIFFORD, H. T. and STEPHENSON, W., 1975. *An introduction to numerical classification*. New York: Academic Press, 229p.

DARNELL, R. M., 1958. Food habits of fishes and larger invertebrates of Lake Ponchartrain, Louisiana, an estaurine community. *Institute of Marine Science Publications, University of Texas*, 5, 353–416.

DELANCEY, L. B., 1984. *An Ecological Study of the Surf Zone at Folly Beach, South Carolina*. M. S. Thesis, College of Charleston, Charleston, S. C. (unpublished).

DELANCEY, L. B., 1987. The summer zooplankton of the surf zone at Folly Beach, South Carolina. *Journal of Coastal Research*, 3, 211–217.

DIAZ, H., 1980. The mole crab *Emerita talpoida* (Say): a case of changing life history pattern. *Ecological Monographs* 50, 437–456.

FINUCANE, J. H., 1969. Ecology of the pompano (*Trachinotus carolinus*) and the permit (*T. falcatus*) in Florida. *Transactions of the American Fisheries Society*, 98, 478–486.

HARRIS, A. H. and C. D. ROSE, 1968. Shrimp predation by the sea catfish *Galeichthys felis*. *Transaction of the American Fisheries Society*, 97, 503–504.

HOBSON, E. S., 1975. Feeding patterns among tropical reef fishes. *American Scientist*, 63, 382–392.

HOBSON, E. S. and CHESS, J. R., 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fishery Bulletin*, 74, 567– 598.

HORN, H. H., 1980. Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morro Bay, California. *Fishery Bulletin*, 78, 759–770.

KALTES, K. H., 1984. Temporal patterns in the three dimensional structure and activity of schools of the Atlantic silverside *Menidia menidia*. *Marine Biology*, 78, 113–122.

KNAPP, F. T., 1949. Menhaden utilization in relation to the conservation of food and game fishes of the Texas Gulf coast. *Transaction of the American Fisheries Society*, 79, 137–144.

LEBER, K. M., 1982. Seasonality of macroinvertbrates on a temperate, high wave energy beach. *Bulletin of Marine Science*, 32, 86–98.

MCDERMOTT, J. J., 1983. Food web in the surf zone of an exposed sandy beach along the Mid-Atlantic coast of the United States. *In*: McLachlan, A. and Erasmus, T. (eds.), *Sandy Beaches as Ecosystems*. Hague: Junk, pp. 529–538.

MCFARLAND, W. N., 1963a. Seasonal plankton productivity in the surfzone of a south Texas beach. *Institute of Marine Science Publications, University of Texas*, 9, 77–90.

MCFARLAND, W. N., 1963b. Seasonal change in the number and the biomass of fishes from the surf at Mustang Island, Texas. *Institute of Marine Science Publications, University of Texas*, 9, 91–105.

MODDE, T. and ROSS, S. T., 1981. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. *Fishery Bulletin* 78, 911–922.

MODDE, T., and ROSS, S. T., 1983. Trophic relationships of fishes occurring within a surf zone habitat in the northern Gulf of Mexico. *Northeast Gulf Science*, 6, 109–120.

MOORE, C. J., 1968. *The Feeding and Food Habits of the Silversides Menidia menidia (Linnaeus)*. M. S. Thesis, University of Delaware, Newark, De. (unpublished).

NELSON, W. G., 1986. Predation and prey population variation in a high energy sand beach macrofaunal community. *Ophelia*, 26, 305–316.

ODUM, W. E., 1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*. *In*: J. Steele (ed.) *Marine Food chains, a Symposium*. Edinburgh: Oliver and Boyd, pp 222–240.

ODUM, W. E. and HEALD, E. J., 1972. Trophic analyses of an estuarine mangrove community. *Bulletin of Marine Science* 22, 671–738.

PEARSE, A. S.; HUMM, H. J. and WHARTON, G. W., 1942. Ecology of sand beaches at Beaufort, North Carolina. *Ecological Monographs*, 12, 135–190.

ROSS, S. T.; MCMICHAEL, R. H., Jr. and RUPLE, D. L., 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. *Estaurine, Coastal and Shelf Science*, 25, 391–412.

SEDBERRY, G. R., 1983. *Food habits and trophic relationships of a community of fishes on the outer continental shelf.* NOAA Technical Report, NMFS SSRF-773, 56 p.

SHERIDAN, P. F., 1978. Food habits of the bay anchovy, *Anchoa mitchilli*, in Apalachicola Bay, Florida. *Northwest Gulf Science*, 2, 126-132.

SIEGEL, S., 1956. *Nonparametric Statistics for the Behavioral Sciences.* New York: McGraw-Hill, 312p.

TAGATZ, M. E., 1968. Biology of the blue crab, *Callinectes sapidus* Rathbun in the St. Johns River, Florida. *Fishery bulletin*, 67, 17–33.

WILLIAMS, A. B., 1984. *Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida.* Washington: Smithsonian Institution Press, 550p.

WOLCOTT, T. G., 1978. Ecological role of ghost crabs, *Ocypode quadrata* (Fabricus) on an ocean beach: scavengers or predators. *Journal of Experimental Marine Biology and Ecology*, 31, 67–82.